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Cone flies, *Strobilomyia* spp. (Diptera: Anthomyiidae), affecting conifer natural regeneration in the Far East

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Abstract: *Strobilomyia* flies are major pests of the cones and seeds of conifers in the Far East. In this region, this apparently monophyletic genus includes 20 species whose larvae specifically develop in the cones of *Larix*, *Abies* and *Picea*. The highest diversity is observed in larch in Northeastern China where the cone resource is shared among seven fly species. However, the precise knowledge of the specific distribution, life cycle and economic impact of *Strobilomyia* spp. has been hindered by taxonomic uncertainties. This paper reviews this important group based on some 108 publications on cone flies in the Far East, and presents additional original data obtained in Central Siberia, Kamchatka, Heilongjiang and northern Yunnan provinces. The fly species related to larch, fir and spruce are successively reviewed according to a common scheme including: distribution, host species and identity; morphology of adults, eggs, larvae and pupae; biology and phenology; damage importance; and forecast and control methods.

Key words: conifer; cone; seed; insect pest; cone fly; *Strobilomyia*

1 INTRODUCTION

Cone flies, or cone maggots, in the genus *Strobilomyia* Michelsen (= *Lasiomma* Stein *Auct. partim* = *Chorthophila* Macquart = *Hylemia* Robineau-Desvoidy) (Diptera: Anthomyiidae) are undoubtedly amongst the most serious cone and seed pests of conifers (Roques *et al.*, 1996a). Species of this apparently monophyletic genus occur mainly in the boreal and mountainous parts of the Holarctic, where larval instars develop exclusively in the cones of various groups of Pinaceae, except pine species (Michelsen, 1988). So far, a total of 20 *Strobilomyia* species are recognized (Turgeon *et al.*, 1994; Skhuravá and Roques, 2000), of which 13 have been observed in the Far East (Popova and Elberg, 1970; Fan *et al.*, 1982; Kamijo, 1993; Roques *et al.*, 1996a; Belova *et al.*, 1998). Nine of the Far Eastern species have been recorded from larches (*Larix* Miller), two from firs (*Abies* Miller), and one from spruces (*Picea* Dietr) while the hosts of an additional species are yet to be determined (Table 1). Only one species (*S. svenssoni* Michelsen) may attack two different conifer genera but this is not definitively established (Michelsen, 1988).

Table 1 *Strobilomyia* spp. recorded in the Far East and their hosts

Strobilomyia species	Hosts			
	Abies	*Larix*	*Picea*	Unknown
S. anthracina (Czerny)			√	
S. baicalensis (Elberg)		√		
S. infrequens (Ackland)		√		
S. laricicola (Karl)		√		
S. lijiangensis Roques & Pan		√		
S. luteoforceps (Fan & Fang)		√		
S. melaniola (Fan)		√		
S. oriens (Suwa)	√			
S. sibirica Michelsen		√		
S. svenssoni Michelsen		√	?	
S. suwai Michelsen				√
S. todocola (Suwa)	√			
S. viaria (Huckett)		√		

The biology of the different species appears similar in general. The eggs are laid on developing cones, the

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specific attack periods being closely synchronised with some phases of cone growth (Yao *et al*., 1991; Roques *et al*., 1995). The larvae pass through three instars but only two are free-living, the first instar remaining within the eggshell. The larvae then tunnel into the cone, feeding on both cone tissues and seeds, and full-grown third-instar larvae drop to the ground where they pupate and overwinter. In most species, a larva can destroy 20 – 30 seeds per cone. As soon as 2 – 3 larvae, possibly belonging to different species, are observed in a cone, its entire seed content is usually destroyed. Thus, cone fly damage may severely hinder the natural regeneration of forested areas as well as the seed crops expected in seed orchards. In the Far East, annual percentages of damaged cones in the range of 50% – 95% are usual in larch (Ivliev, 1973; Fang *et al*., 1988, 1989; Yao *et al*., 1991; Sun *et al*., 1994). In addition, the fly populations are capable of surviving years in which cones are unavailable (masting is common in conifers) because a variable part of the overwintering puparia extend the winter diapause for an additional 1 – 4 year period (Roques, 1988).

Precise knowledge of the specific distribution, life cycle (including importance of prolonged diapause) and damage of *Strobilomyia* spp. has been hindered by taxonomic uncertainties. Until the 1980's, most cone fly damage observed on larch all over Eurasia was erroneously attributed to a single species, *Strobilomyia* (*Lasiomma*) *laricicola* Karl (Petrenko, 1963, 1965; Rozhkov, 1966; Galkin, 1971a; Elin, 1973) whereas it was in fact due to the joint attack of several species. For example, in Central Siberia, damage by *S*. *laricicola* was recorded from the territories of Evenkiya (Galkin and Nadeev, 1966), Khakasiya (Luchinin and Govzich, 1971), and Zapadnyi Sayan (Zemkova, 1965; Rozhkov, 1966; Petrenko and Zemkova, 1967) but further investigations proved that 2 additionnal species (*S*. *infrequens* and *S*. *sibirica*) may dominate *S*. *laricicola* for cone occupancy in some of these areas (Belova *et al*. 1998). This confusion led to major misunderstandings of the fly life cycle. In Kamchatka, the duration of the egg-laying period of *S*. *laricicola* was considered to extend over more than two months (Ivliev *et* Kononov, 1962; Efremova and Zhuravlev, 1966; Efremova, 1971) whereas this duration actually involved oviposition by four species at least. Damage to fir cones and spruce cones in the Holarctic was similarly attributed to S. (*Lasiomma*) *abietis* (Huckett) and to *S*. *anthracina* (Czerny) respectively.

After Michelsen meticulously revised the taxonomy of cone flies and erected the genus *Strobilomyia* in 1988, the development of genitalia examination as a routine standard for specific identification resulted in a more precise information on the distribution and biology of cone flies (Sun *et al*., 1996b). Large surveys were thus developed in Northern China (Fang *et al*., 1980, 1988, 1989; Fan *et al*., 1982; Fang, 1987, 1993; Yao *et al*., 1991, 1993; Sun *et al*., 1994; Roques *et al*., 1996a; Pan and Roques 2001), Central China (Zhang and Li, 1991, 1994), Southwestern China (Roques *et al*., 1996a), Japan (Kamijo, 1993), and Central Siberia (Belova *et al*., 1998). Keys were developed for specific identification of eggs, larvae, and puparia of larch cone flies (Sun *et al*., 1993, 1996a; Fan and He, 1995). A number of studies detailed fly biological patterns regarding the synchronization of adult emergence with cone phenology (Yao *et al*., 1991; Roques *et al*., 1995; Sun *et al*., 1996a; Yan *et al*., 1998), and host recognition using visual cues (Roques *et al*., 1995; Yan *et al*., 1997a) and olfactory cues (Yan *et al*., 1999a, 1999b; Sun *et al*., 2000), as well as forecast and control methods (Gao, 1992; Liu, 1993; Sun *et al*., 1995a; Roques *et al*., 1996b; Sun *et al*., 2000). However, the data remained fragmentary because large areas of the Far East were not accurately sampled or confusion between *S*. *laricicola* and other *Strobilomyia* species persisted (e.g., Tyul'panova *et al*., 1990, 1991).

Moreover, recent preliminary genetic investigations of *Strobilomyia* spp. using mtDNA revealed that the morphology of the genital apparatus may not accurately reflect the degree of genetic differentiation between species or populations of the same species (Sachet, unpublished data).

Therefore, the aim of this paper is to synthesize the available literature on cone flies in the Far East in order

to clarify the host plants, distribution, and life cycles of the different *Strobilomyia* species present in the region. Wee also include the results of surveys we carried out in the Western Sayans (1996), Kamchatka (1997), and northern Yunnan (1996 – 2001) (Battisti *et al*., 1998; Pan and Roques, 2001) and successively describe the fly species related to larch, fir and spruce.

2 LARCH CONE FLIES

Since the 1960's, a total of 101 papers have been published on larch cone flies in the Far East. Only 53 of these papers considered species other than *S. laricicola* but they present sufficient data to clarify the most important biological patterns associated with each species.

2.1 Distribution, hosts and species identity

Among the nine species recorded from the Far East, five have a much wider distribution range (Fig. 1). They include:

1) *S. laricicola* (Karl), a widespread Palearctic species continuously observed from Western Europe to Kamtchatka and Japan, including Central and Eastern Siberia, Mongolia, and the Chinese provinces of Inner Mongolia, Heilongjiang, Liaoning, Jilin, Shanxi and Hebei (Zonova, 1935; Florov, 1951; Rozhkov, 1965; Popova and Elberg, 1970; Suwa, 1971; Yanovski, 1971; Yamada *et al*., 1972; Ivliev, 1973; Stadnickii *et al*., 1978; Fan *et al*., 1982; Michelsen, 1988; Fang *et al*., 1980, 1988, 1989; Kamijo, 1993; Zhang and Li, 1994; Roques *et al*., 1996a; Belova *et al*., 1998). It attacks all the larch species growing in the region: *Larix sibirica* Ledeb., *L. czekanowskii* Szaf., *L. gmelini* Rupr. (Kusen.), *L. leptolepis* (Sieb. *et* Zucc.) Gord., *L. cajanderi* Mayr, *L. olgensis* Henry, and *L. principis-rupprechti* Mayr. (Yamada *et al*., 1972; Stadnickii *et al*., 1978; Kamijo, 1993; Zhang and Li, 1994; Roques *et al*., 1996a).

2) *S. infrequens* (Ackland), another widespread Palearctic species observed from England to Kamchatka, including Central and Eastern Siberia, and the Chinese provinces of Inner Mongolia, Heilongjiang, Liaoning, Jilin, Shanxi and Hebei (Popova and Elberg 1970; Stadnickii *et al*., 1978; Fan *et al*., 1981; Fang *et al*., 1980, 1988, 1989; Michelsen, 1988; Zhang and Li, 1994; Roques *et al*., 1996a; Belova *et al*., 1998). However, it has not yet been recorded from Japan (Yamada *et al*., 1972; Kamijo, 1993). Larch hosts are similar to these of *S. laricicola*.

3) *S. sibirica* Michelsen, a Eurosiberian species observed in the range of the Siberian larch, *L. sibirica*, from Eastern Scandinavia to Central Siberia (Krasnoyask area, Khakassia) (Popova and Elberg 1970; Stadnickii *et al*., 1978; Michelsen 1988; Belova *et al*., 1998); we observed it recently in Heilongjiang (Table 2). It attacks *Larix gmelini*, *L. sibirica*, and *L. sibirica x L. decidua*.

Table 2 Relative importance(%) of the different *Strobilomyia* species in total adult emergences obtained during 1998 to 2000 from pupae collected at Esso, Kamchatka, July 1997 ($n = 450$) and Jagedaqi, June 1997 ($n = 259$)

Species	Esso	Jagedaqi
S. baicalensis	15.4	3.5
S. infrequens	23.8	6.6
S. laricicola	6.2	39.8
S. luteoforceps	–	–
S. melaniola	–	45.6
S. sibirica	–	0.8
S. svensonni	–	3.9
S. viaria	55.3	–

4) *S. viaria* (Huckett), a trans-Beringian species, that has been observed from northwest of America (Canada, USA) (Michelsen, 1988) to the Baikal area and Yakutia (Popova and Elberg, 1970; Michelsen, 1988), including Kamtchatka (Table 2) and South Korea (Suh *et al*., 1991). In Asia, it attacks *L. gmelini*, *L. sibirica* and *L. cajanderi* (Roques, unpublished results).

5) *S. svenssoni* Michelsen, reported in Sweden, Mongolia (Michelsen 1988), Central Siberia (Belova *et al*., 1998) and Northeastern China (Da Khinggan Mountains) (Sun *et al*., 1995b; Roques *et al*., 1996a). The only certain host is *Larix gmelini*, from which adults were reared in Northern China (Roques *et*

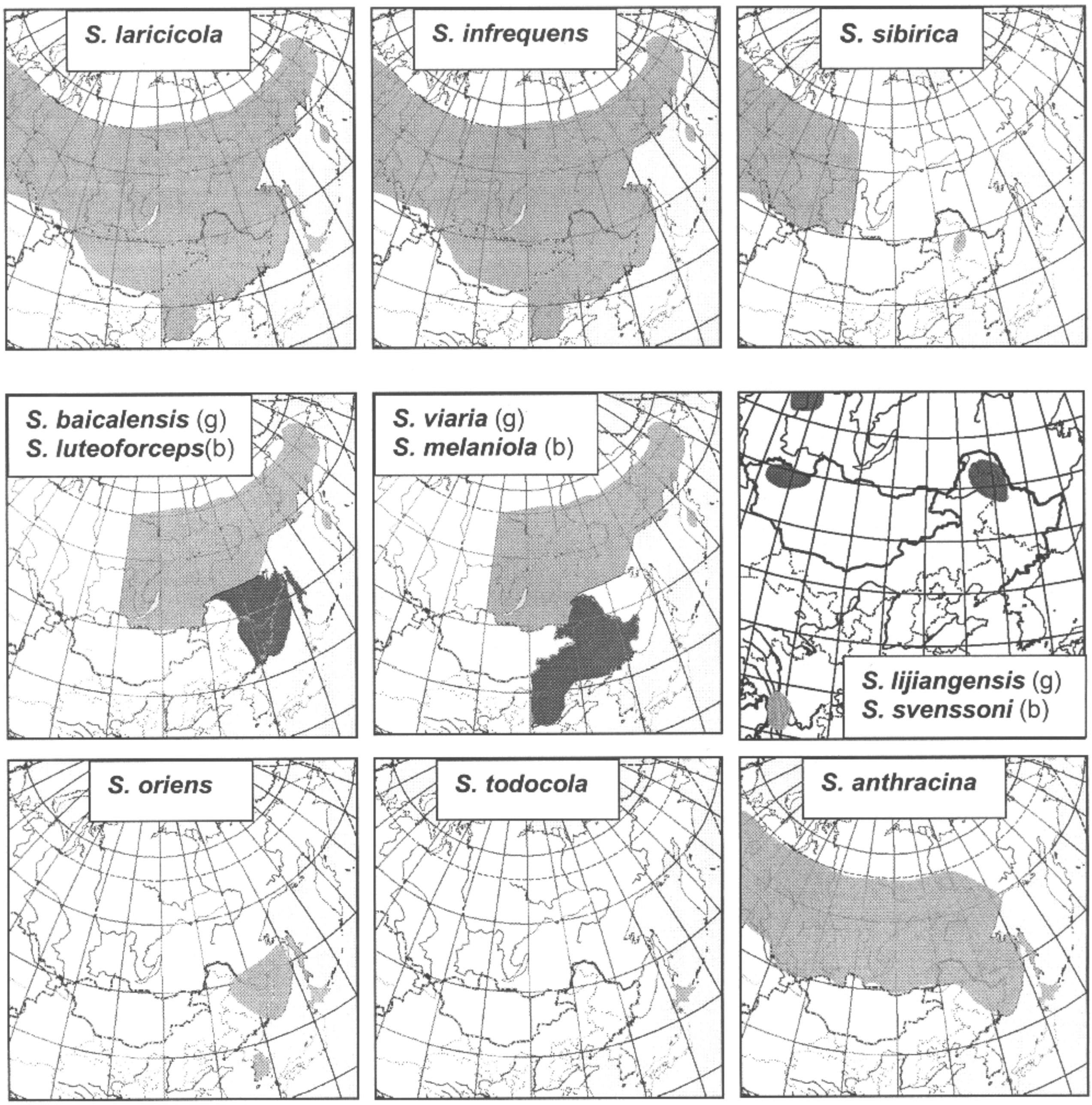

Fig. 1 Distribution maps of *Strobilomyia* cone flies in the Far East
b: black; g: grey

al., 1995; Sun *et al*., 1995b) but *Picea* abies and *P*. *obovata* are suspected (Belova *et al*., 1998; Michelsen, 1988).

The four other species of larch cone flies seem endemic to Eastern Asia (Fig. 2). They consist of:

6) *S*. *baicalensis* (Elberg), a Northasian species observed from Central Siberia to Kamtchtka, including Eastern Siberia (the Lake Baikal area and Yakutia) and Northeastern China (Inner Mongolia, Heilongjiang) (Fan, 1988; Michelsen 1988; Popova and Elberg 1970; Roques *et al*., 1996a; Stadnickii *et al*., 1978). Known hosts are *L*. *sibirica*, *L*. *czekanowskii*, *L*. *gmelini*, *L*. *olgensis*, and *L*. *cajanderi*.

7) *S*. *melaniola* (Fan), that has been recorded from Northeastern China (Liaoning, Jilin, Heilongjiang, Inner Mongolia) (Fan *et al*., 1982, 1990; Yao *et al*., 1991, 1992; Liu *et al*., 1994a; Roques *et al*., 1996a; Sun *et al*., 1996c) and Central China (Shanxi, Hebei) (Zhang and Li, 1994). Attacks

concern *L. gmelini*, *L. olgensis* Henry, and *L. principis-rupprechti* Mayr (Roques *et al*., 1996a; Zhang and Li, 1994).

8) *S. luteoforceps* (Fan & Fang) (= *Lasiomma jurtschenkoi* Elberg) that is apparently limited to the Far East, having only been recorded from the Northeastern part of China (Xiao Khinggan Mountains of Heilongjiang) (Fan and Fang, 1981; Fan *et al*., 1982; Yao *et al*., 1991), from the Primorié and Amur region of Russia, and from Sakhalin (Stadnitckii *et al*., 1978). It attacks *L. gmelini*, *L. olgensis*, and *L. cajanderi*.

9) *S. lijiangensis* Roques and Pan, only observed in the mountains of northern Yunnan (Dali, Lijiang, Lugu, Zhondian, Deqên) (Roques *et al*., 1996a). It develops on *L. potaninii* Batalin var. *mastersiana* Law.

Thus, the larch cone resource appears to be shared among four cone fly species in Central and Eastern Siberia as well as in Kamtchatka, whilst five species are likely in Primorié, and seven species occur in Northern China (Table 2). In contrast, only one species was found in South Korea (Suh *et al*., 1991) as well as in Japan in spite of meticulous investigations in the latter country (Kamijo, 1993). The species number in the Far East is significantly higher than that observed in Europe, which has only 3 species (Skhuravá and Roques, 2000), suggesting that this region, and probably Northeastern China, is the center of origin for larch cone flies. In northern Yunnan and Tibet, the observation of different patterns of cone damage suggested that additional *Strobilomyia* species exist besides *S. lijiangensis* on Hymalayan larch (Pan and Roques, 2001).

However, some questions remain about the specific identity of some of these species. Whereas Fan *et al*., (1982, 1990) considered *S. melaniola* a distinct species, Michelsen (1988) synonymized it with *S. viaria*. Recent mtDNA analyses tended to confirm Michelsen's assumptions, the genetic distances between *S. viaria* from Kamchatka and *S. melaniola* from Heilongjiang, as well as *S. sibirica* from Central Siberia, appearing very limited. On the basis of morphological and biological relatedness, these 3 species have been gathered in the same *melania* group by Michelsen (1988) and may actually correspond to a unique species. On the other hand, these analyses suggest that the Far Eastern populations of *S. laricicola*, and to a lesser extent those of *S. infrequens*, are genetically divergent from those observed in Western Europe and may constitute a separate species.

2.2 Morphology of adults, eggs, larvae and pupae

Adults are typical, small to medium-sized anthomyiid flies of blackish colour. Wing length ranges 3.3 – 5.7 mm. Sexual dimorphism is noticeable, males being easily identified by adjacent eyes whereas females' eyes are separated by a broad stripe. The ground colour of the body is blackish with a grey or bluish-grey pruinosity. Haustellum is short and conical in *S. laricicola* and cylindrical in other species. The base of wings is yellowish to orange-brown except in *S. laricicola*, *S. svenssoni* and *S. viaria*. The species are very difficult to separate by external examination of adults, and genital dissection must be systematically used for accurate identification, especially of trapped flies. All of the terminalia of the Far Eastern species have been described (Fan *et al*., 1982, 1990; Michelsen, 1988; Roques *et al*., 1996a; Sun *et al*., 1996b). In the male, diagnosis is based on both the shape and pilosity of the apex of the cercal plate, the shape of the two elongated surstily and the orientation of their apical incision, and the arrangement of the bristles on the 5th sternite (Fig. 2). In the female, idenfication is based on both the shape of the cerci and that of the sclerites present on tergite and sternite of the abdominal segments Ⅶ, Ⅷ, and Ⅸ (Fig. 3).

Egg morphology was precisely identified in six of the fly species (Sun *et al*., 1996a). The egg of *S. laricicola* is oval with two rounded extremities. Length of 1.45 mm on average, and approximately 2.75 times longer than broad, it is the largest egg of larch cone flies. Egg colour varies from creamy white to yellowish with the apex usually darker, and the chorion is noticeably marked by steeply elevated zig-zag ridges. The egg of *S. infrequens* is spindle-shaped with an acute base. It averages 1.37 mm in length and is about 3.9 times

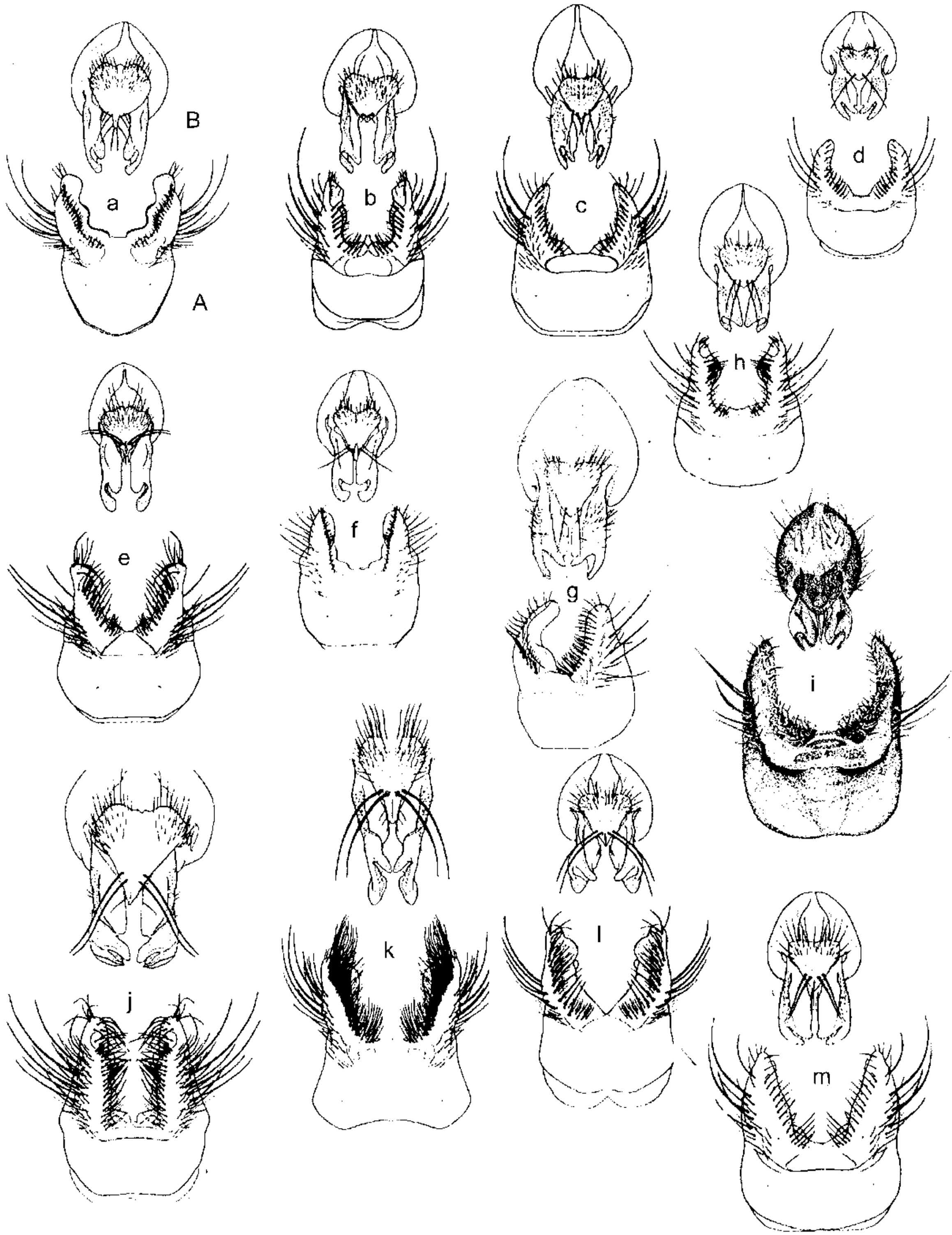

Fig. 2 Male genitalia of *Strobilomyia* cone flies observed in the Far East

a. *S. laricicola*; b. *S. infrequens*; c. *S. sibirica*; d. *S. viaria*; e. *S. svenssoni*; f. *S. baicalensis*; g. *S. melaniola*; h. *S. luteoforceps*; i. *S. lijiangensis*; j. *S. oriens*; k. *S. todocola*; l. *S. suwai*; m. *S. anthracina* (from Michelsen, 1988, modified, except "g" from Fan *et al.*, 1990, modified and "i" from Roques *et al.*, 1996, modified). A: sternite V; B: epandrium, surstylus and cercal plate.

longer than broad. Egg colour is ivory white, and the chorion is perfectly smooth. The egg of *S. baicalensis* is oval. It measures 1.25 mm in length and is about 2.25 times as long as wide. Egg colour is yellowish,

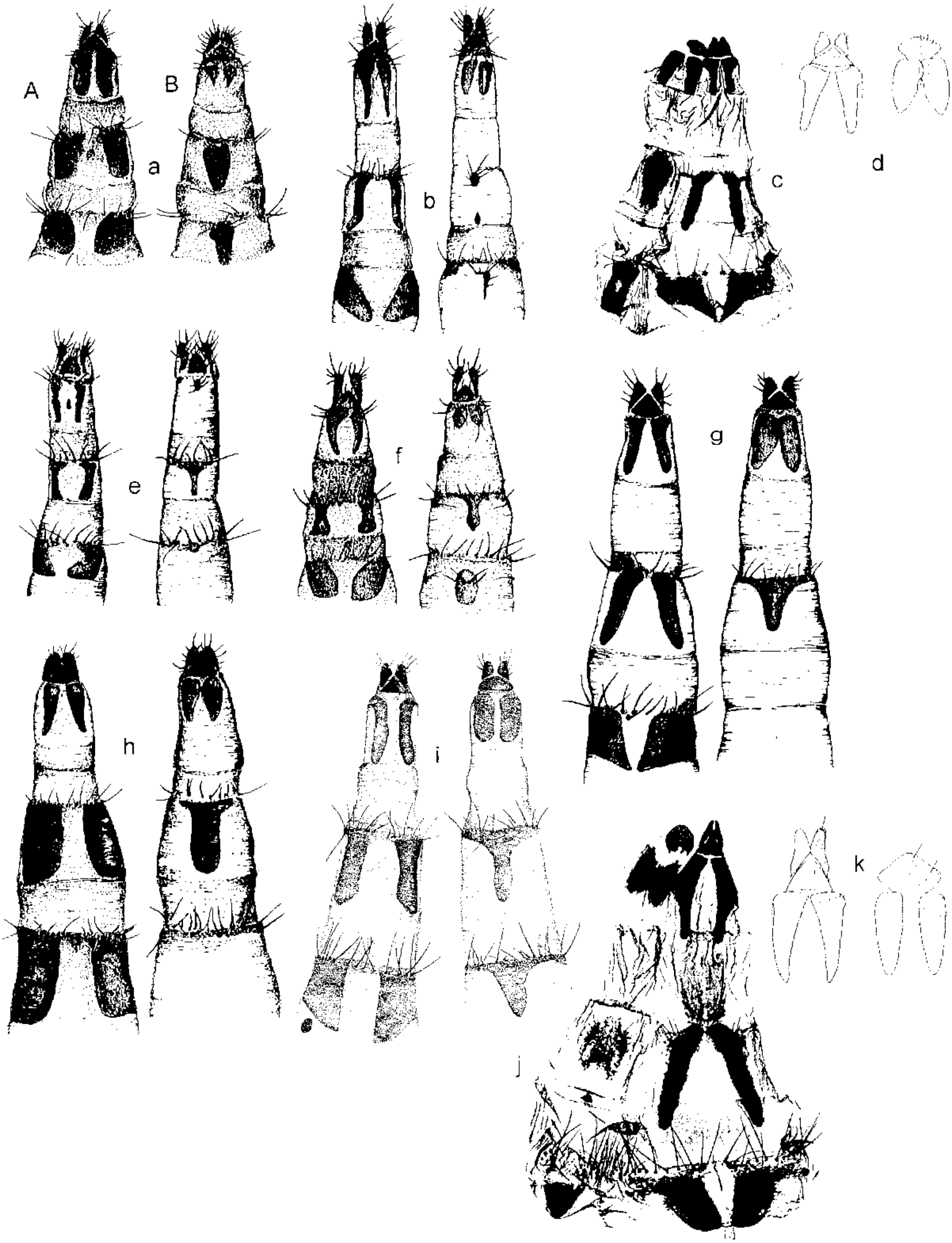

Fig. 3 Ovipositor of *Strobilomyia* cone flies observed in the Far East

a. *S. laricicola*; b. *S. infrequens*; c. *S. sibirica*; d. *S. viaria* (segments Ⅷ – Ⅸ); e. *S. svenssoni*; f. *S. baicalensis*; g. *S. melaniola*; h. *S. luteoforceps*; i. *S. lijiangensis*; j. *S. oriens*; k. *S. anthracina* (segments Ⅷ – Ⅸ) (from Sun *et al*., 1996b, modified except c, d, j, k- from Michelsen, 1988, modified and i- from Roques *et al*., 1996, modified). A: tergites Ⅶ – Ⅸ; B: sternites Ⅶ – Ⅸ.

and the chorion surface is deeply wrinkled, with a very irregular overlying reticulum formed by longitudinal furrows interwoven with transverse rounded ridges. The egg of *S. melaniola* is elongate-oval with a flat apex and a

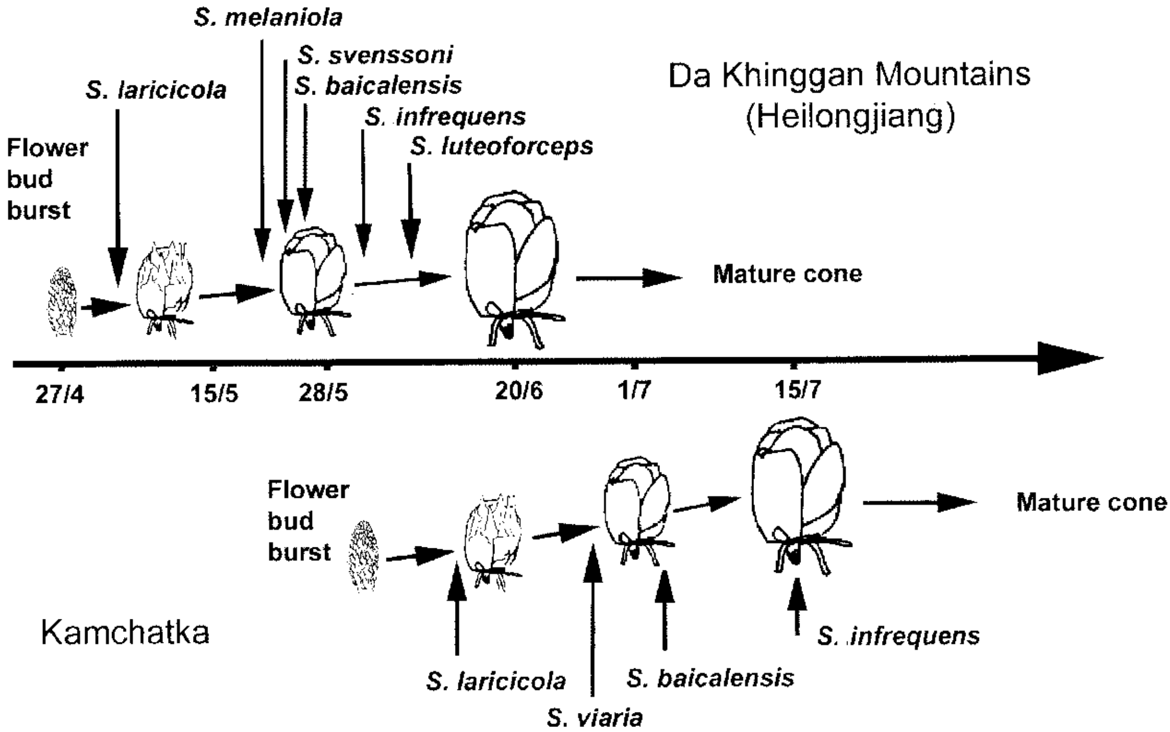

Fig. 4 Phenological relationships between larch cone development of *Larix gmelinii* and specific attacks by *Strobilomyia* spp. in Northern China (from Yao *et al*., 1991, modified) and Kamchatka

rounded base. It measures 1.25 mm in length, and is 3 to 3.7 times as long as wide. Egg colour is ivory white as in *S. infrequens* but the chorion is moderately wrinkled, showing a characteristic raised network of columnar pentagonal cells. The egg of *S. svenssoni* is obovate with a base larger than the apex. It measures 1.18 mm in length, and is only 1.75 times as long as wide at its greatest width. Egg colour is creamy white to yellowish, and the chorion is marked by longitudinal lines of characteristic prominences in the shape of two raised funnels with radiating and anastomosing processes. The egg of *S. luteoforceps* is oval. It measures only 0.8 mm in length, and is 2.5 times as long as wide. Egg colour is creamy white, and the chorion is marked by longitudinal lines of rasp-like prominences from which faint linear processes develop transversally.

Larva body is elongated, legless, with a sclerified cephalopharyngial skeleton at the anterior extremity, and 2 large spiracular tubercules surrounded by a circle of papillae at the anal extremity (Fig. 5). *Strobilomyia* larvae can be confused with these of *Earomyia*, belonging to another dipteran family, Lonchaeidae, which may coexist in the same cone. However, lonchaeid larvae are easily distinguished by smaller size and a smooth hind end with the posterior spiracles located on definite, pigmented prominences without surrounding papillae (Skhuravá and Roques, 2000). The 2nd-instar larva of *Strobilomyia* is quite transparent on hatching, and its length ranges from 1 – 1.5 mm. The white to yellowish 3rd-instar larva measures 6.0 – 9.0 mm in length depending on species. The shape of the cephalopharyngian skeleton provides diagnostic characters for specific identification of the 3rd-instar larvae of four of the species (*S. baicalensis*, *S. infrequens*, *S. laricicola*, and *S. melaniola*) (Yamada *et al*., 1972; Fan and He, 1995). Fan and He (1995) also showed that the distance between the two supra-anal papillae compared to the width of the anal plate allows the separation of *S. baicalensis* (distance larger than plate width), *S. laricicola* (distance smaller or at most equal), and *S. melaniola* (distance much smaller). In addition, the number of stigmae of the anterior spiracles has been shown to differ between *S. baicalensis* and *S. melaniola* (both 11 stigmae), *S. laricicola* (15 – 17 stigmae

in Europe according to Skhuravá and Roques, 2000; 10 in China), and *S*. *infrequens* (13 – 15 stigmae) (Skhuravá and Roques, 2000). On the other hand, Sun *et al*., (1993) separated the puparia of *S*. *laricicola* and *S*. *infrequens* by comparing the distance between spiracles to the width of a spiracular process.

2.3 Biology and phenology

A close synchrony has been shown in Northeastern China between cone development of *L*. *gmelini* and the oviposition of the 6 related fly species, which follow one another in a given order (Yao *et al*., 1991). In the Da Khinggan Mountains, the temporal sequence of cone attack first involves a group of precocious species (*S*. *laricicola*), then a group of intermediary species (*S*. *melaniola*-*S*. *svenssoni*-*S*. *baicalensis*) and, finally, a third group of late species (*S*. *infrequens*-*S*. *luteoforceps*) (Fig. 4). Thus, the overall oviposition period of cone flies lasts about 1 month and a half, from 5 May to 15 June, which corresponds to the early phases of cone development when cones tissues are soft. Although their emergence periods largely overlap, each species has a different oviposition pattern as indicated by both the colonization of distinct phases of cone development and the selection of different oviposition sites. As a rule, the newly emerged adults need at least 2 – 3 weeks to mature before mating and oviposition begins. The emergence of the earliest species, *S*. *laricicola*, coincides with cone bud burst, and oviposition is observed two weeks later. The female inserts the egg singly, or more rarely in groups of 2 – 3, within the cone pedicel. Therefore, the egg is visible only when the cone is removed from its stalk. *S*. *melaniola* oviposition starts as soon as the ovuliferous scales become externally visible but are still covered by the bracts, and lasts about 2 weeks. Eggs are inserted between the scales and bracts, but they remain externally visible. *S*. *svenssoni* lays eggs when the scales become larger than the bracts. Eggs are found at the base of cones on the external side of scales, and are visible externally. *S*. *baicalensis* oviposits at the same time but the eggs are inserted between scales, mostly at the base of cones, and are not visible unless cones are dissected. Oviposition of *S*. *infrequens* is delayed and begins at the onset of cone lignification, when bracts are quite entirely covered by scales. The eggs are laid on the inner side of the scales and are visible only when the cones are dissected. Finally, *S*. *luteoforceps* is the last species to emerge. They probably lay eggs at the end of cone growth but the oviposition patterns are not known. Yan *et al*. (1998) calculated the temperature sums necessary for egg development of some fly species in Northeastern China.

Similar species-specific egg-laying patterns have been observed in Central Siberia and Kamchatka, where *S*. *melaniola* is replaced by *S*. *sibirica* and *S*. *viaria* respectively (Fig. 3). The overall duration of the oviposition period of these four species explains why Efremova and Zhuravlev (1966) and Efremova (1971) considered that eggs of *S*. *laricicola* could be found on cones during two months in Kamchatka.

Although the specific patterns of larval damage have not yet been identified, some general information is available. Egg development lasts 5 – 7 days in all species. Then, the first-instar larva develops within the egg for 4 – 8 days. The second-instar larva enters the cone tissues at the place where the egg was laid. It tunnels down the corresponding scale, reaches the scale base and destroys the basal seeds. Then, the larva spirals round the cone axis, feeding on seeds during its course. Damage patterns seem to depend on the egg position in the cone. Larvae hatched from eggs laid in basal parts of the cone tunnel up to the middle part of the cone (Fig. 5a). Those from eggs laid in the apical part tunnel down to the middle and those from the middle part damage either the upper or the lower part of the cone. The second instar lasts about 10 – 15 days. The third-instar larva generally develops in a similar way, and makes larger galleries tunnelling round the axis. Unlike other fly species, larvae of *S*. *laricicola* enter the cone axis during this stage except in Japan (Kamijo, 1993). This typical damage can thus be easily recognized (Fig. 5b). The third larval instar lasts 15 – 25 days within the cones. The full-grown larvae then bore a hole and drop to the ground, generally during days of rainfall. Larvae vacate cones from mid-June to mid-August, depending on both species, latitude and weather

conditions. However, Kamijo (1993) noticed that 24% to 81% of the larvae of *S. laricicola* may pupate within the cone in Japan, the percentage of pupation being inversely related to the importance of rainfall during late June, the period of larval exit. When on the ground, larvae then build a puparium in the upper soil layer, 3 – 10 cm below the ground surface, where they overwinter.

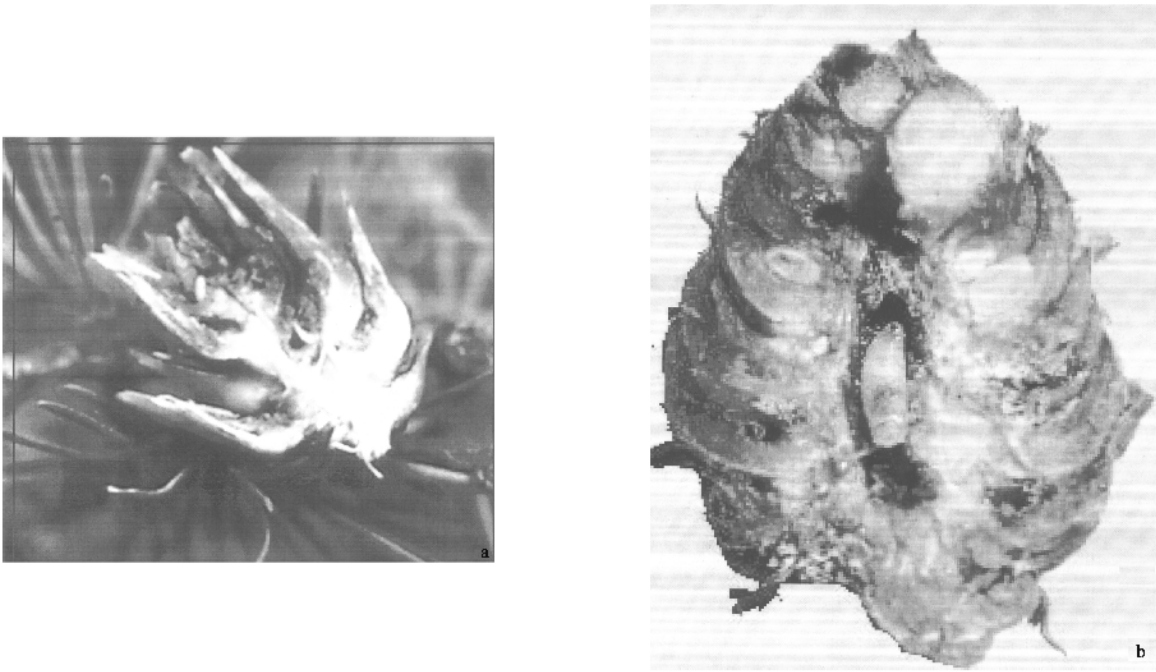

Fig. 5 Cone damaged by a larva of *Strobilomyia* spp.
a. cross- section of a cone of *Larix gmelini* damaged by a larva of *Strobilomyia melaniola*;
b. larva of *Strobilomyia laricicola* attacking the axis of a larch cone.

In all areas, some adults emerge the following year but a variable part of the population remains in prolonged diapause (Iurchenko, 1970a). Although no specific data exist about prolonged diapause, it is likely that fly species differ in patterns of prolonged diapause, which also depends on latitude and annual fluctuations in cone crop. In the Da Khinggan Mountains of China, 84% of the 1993 fly generation remained in prolonged diapause in 1994, but most adults of *S. melaniola* and *S. infrequens* emerged at that time while those of other species did not. As a rule, the overall development of *S. luteoforceps* lasts 2 years, at least, in Primorié in relation with the periodicity of larch cone crops (Stadnitckii *et al.*, 1978). In Kamtchatka, the development cycle of cone flies usually extends to 3 years, which represents the mean interval between two good larch crops (Efremova, 1971).

2.4 Damage importance

As a direct result of feeding activity, a larva can destroy 20 – 30 seeds per attacked cone, i.e., 50% – 70% of the cone seed content in a larch species with large cones (*L. sibirica*) but nearby 100 % of the seed content in a species with small cones (*L. gmelini*) (Iurchenko, 1970b; Stadnickii *et al.*, 1978; Yao *et al.*, 1991). Moreover, precocious resumption of cone growth as well as cone dehydratation caused by larvae usually result in an additionnal abortion of undamaged seeds, especially when the cone axis has been excavated by *S. laricicola* (Skhuravá and Roques, 2000). As soon as 2 – 3 larvae, possibly belonging to different species, are observed in a cone, the whole seed content is destroyed. Thus, seed damage due to larch cone flies largely limits the potential for natural regeneration of larch forests in the Far East. Moreover, cone flies usually destroy a large part of the annual seed crop in seed orchards.

Only a few data exist about specific damage because of difficulties in larvae identification but some general trends are apparent. The dominant species, and the subsequent impact, largely varies with site, cone

crop size and years. *S. laricicola* is undoubtely a major seed pest of larches but its impact was probably overestimated before the 1980's. Damage is apparently more important in boreal and high-altitude situations (Michelsen, 1988). The percentage of damaged cones can reach up to 70% in natural larch stands of Siberia and Japan but largely varies with cone crop size. When the cone crop is heavy, usually less than 15% of the cones are attacked whereas damage is generally higher than 50% when there are a few cones (Yamada *et al*., 1972; Stadnickii *et al*., 1978; Kamijo, 1993). In Northeastern China, some studies tended to minimise the impact of *S. laricicola* with regard to that of other fly species (e.g., Yao *et al*., 1991). This may correspond to a bias due to late cone samplings because *S. laricicola* is the earliest species to leave the cone. Recent data obtained from Heilongjiang showed that this species could represent about 40% of the flies in some cases (Table 2). In contrast to the European situation where it constitutes a minor pest (Skhuravá and Roques, 2000), *S. infrequens* is a major seed pest in the Far East, where it accounts for about 1/3 of the fly damage in both Central Siberia, Kamchatka and Northeastern China (Belova *et al*., 1998; Yao *et al*., 1991; Table 2). *S. baicalensis* is a major pest in Northeastern China and Kamchatka where it can attack up to 50% of the cones (Yao *et al*., 1991; Table 2). *S. luteoforceps* seems a problem only in Primorié where the percentage of damaged cones varies from 50% during years of large cone crops to 95% – 100 % during years of light crops (Stadnickii *et al*., 1978). *S. melaniola* often dominates the cone fly complex in Northern China where it frequently accounts for 40% to 70% of cone damage (Yao *et al*., 1991; Roques *et al*., 1995; Sun *et al*., 1996c; Table 2), whereas *S. viaria* is a major pest in Kamchatka where it attacks 25% – 40 % of cones (Table 2). *S. sibirica* is usually dominant in Central Siberia (Belova *et al*., 1998), whereas no serious damage by *S. svenssoni* has been recorded.

The additive impact of the fly species usually leads to overall damage higher than 40% of the cone crop. Ivliev (1973) noticed a persistent damage at a rate of 75% – 90% in Kamchatka, the lower part of the Amur Basin and Magadan region (see also Zakharova, 1971), even when cones were abundant, and cone damage may reach up to 95% – 100% during years of light crops. Similarly, Battisti *et al*. (1998) estimated that 77% – 100% of the cones were attacked at Esso, Kamchatka. In contrast, Ivliev (1973) indicated lower damage near Khabarovsk, in Primorié (Maritime Territory), and especially near Okhotsk where it did not exceed 20% – 30% of cones. In Central Siberia, the yearly damage to the cone crop of Siberian larch is never less than 40% – 60%, and can be up to 80% – 95% (Stadnitckii *et al*., 1978) in small crops. Petrenko (1963, 1965), Zemkova (1965), and Popova (1969) observed similar damage values in Yakutia, Western Sayan, and the Lake Baikal area, respectively. In Japan, 45% – 86% of the cones of *L. leptolepis* are destroyed during poor crop years (Kamijo, 1993). A long-term survey of stands selected for production of *L. gmelini* seeds in Inner Mongolia and Heilongjiang revealed that the percentage of cone damage varied with the annual fluctuations in cone crop (Yao *et al*., 1991, 1993; Zhang *et al*., 1991a). Cone damage increased when the cone crop decreased from one year to the next, and conversely. However, the percentage of cone damage never decreased below 69%, and generally varied between 80% and 99%. In these locations, the overall fly population appears to grow as soon as the size of the current cone crop exceeds that of the larval population present the year before. Thus, total cone damage is significantly higher in the Far-East than in other Palearctic areas (e.g., the Alps) (Roques, 1988), probably because the higher number of cone flies species results in a constant high degree of cone occupancy.

2.5 Forecasting and control methods

Several predictive models have been developed in Northeastern China to forecast overall damage by cone flies (Xu and Zhang, 1991; Liu and He, 1994) but these do not forecast the respective part played by the different *Strobilomyia* species. Visual traps were used for specific monitoring of cone flies in Northeastern China (Gao *et al*., 1991b; Roques *et al*., 1995), Yun-

nan (Pan and Roques, 2001), Kamtchatka (Battisti *et al*., 1998), and Central Siberia (Western Sayan) (Battisti *et al*., 1998). Species- and sex-specific responses of flies to trap colour and trap position were observed. Traps coloured in yellow with or without purple stripes were effective in capturing males of most *Strobilomyia* species, except *S*. *laricicola*, but not females (Roques *et al*., 1995). However, blue traps appeared significantly more attractive in all areas, especially for sexually immature females. The fly species responded differently to trap position, probably because of differences in foraging patterns. In Northeastern China, blue sheets fixed on trunks seemed preferred by females of *S*. *infrequens*, whilst traps hung at the periphery of tree crowns were more attractive for those of *S*. *melaniola*. *S*. *baicalensis* showed no clear preference for either trap position (Roques *et al*., 1995). *S*. *viaria* behaved similarly as *S*. *melaniola* in Kamchatka and the Western Sayan (Battisti *et al*., 1998) as did *S*. *lijiangensis* in Yunnan (Pan and Roques, 2001).

Traps baited with various chemicals, especially vinegar, have also been used in China (Fang *et al*., 1980; Gao *et al*., 1991a). More recently, studies have focused the role of cone volatiles, especially terpenoids, in the host recognition process. Significant differences in cone damage were related to different cone volatile profiles in *Larix gmelinii* (Yan *et al*., 1999a). Volatile emission was also shown to change with the development of larval damage (Guo *et al*., 1999). These results led to proposing the use of cone-emitted terpenoids either as attractants or repellents (Sun *et al*., 2000). However, results of field spraying of cones with the suggested blends have not yet been conclusive (Yan *et al*., 1999b).

The pathogenicity of several entomopathogenic fungi (*Beauveria bassiana*, *B*. *tenella* and *Paecilomyces farinosus*) was tested in Siberia (Tyul'panova, 1965; Tyul'panova and Tyul'panov, 1972; Tyul'panova *et al*., 1975, 1990, 1991) and Northeastern China (Gao *et al*., 1991e). Tyul'panova *et al*., (1990) noticed that 72% of *Strobilomyia* larvae leaving cones to pupate in Siberia were killed by *P*. *farinosus*.

Only a few natural enemies of larch cone flies have been recorded in the Far East and, usually, the *Strobilomyia* species parasitized or preyed on has not been accurately identified (Stadnitckii *et al*., 1978; Zhang *et al*., 1991b). The parasitoids are all hymenopterans. They consist of an egg parasite, *Trichogramma* sp. (Trichogrammatidae), three ovo-larval parasitoids of the Braconidae family (*Phaenocarpa notabilis* Stelt in the Amur region, *Phaenocarpa* sp. aff. *mariae* Hal. in Northern China and in the Amur region, and *P*. *seitneri* Fahr. in the Irkustk region and Heilongjiang), four larval endoparasitoids of Cynipidae family (*Seitneria austriaca* Tavar. in Siberia and Heilongjiang, *Sarothrus punctatus* Beliz. and *Melanips opacus* Htg. in the Amur region, *Sarothrus* sp. in Northern China), and five larval ectoparasitoids of Ichneumonidae family (*Asyncrita rufipes* Först. in the Baikal area, *Attractodes foveolatus* Grav. in Kamtchatka and Heilongjiang, *Attractodes* sp. aff. *liogaster* Thoms. and *Phygadenon* sp. in the Amur region, and *Scambus* sp. in Kamtchatka). A larval predator, *Spermatolonchaea viridana* Meig. (Diptera: Lonchaeidae) is widely distributed in Siberia and Northern China, and can contribute for 35% of maggot mortality in some years in Heilongjiang. Another lonchaeid predator, *Lonchaea* sp., has been observed in Kamtchatka. None of these natural enemies has yet been used for biocontrol.

Various chemical treatments using aerial and ground sprays were investigated in Siberia (Galkin, 1968, 1971b; Iurchenko, 1971, 1973; Kobzar' *et al*., 1971; Aukshitikal' nene, 1981) and Northern China (Gao *et al*., 1991c). However, most studies referred to *S*. *laricicola* and did not consider the other fly species. This may explain why the treatment results are usually variable. In contrast, systemics appear to in effectively controlling cone flies. Implantation of larch tree trunks with capsules of acephate decreased the number of fly-damaged cones in a seed orchard of Heilongjiang by 85% (Roques *et al*., 1996b). Chi *et al*. (1999) also noticed that spraying cones with insect growth regulators at the peak of adult emergence reduced damage by 20% – 80%, and by 35% – 40% when the spray was done at the peak of egg-laying.

Finally, Integrated Pest Management methods

combining all these techniques were recently proposed in Northeastern China (Gao, 1992; Sun *et al*., 2000).

3 FIR CONE FLIES

A very limited number of papers (9 papers) have dealt with fir cone flies in the Far East.

3.1 Distribution, hosts, and specific identity

Fir cone flies have been precisely identified only in Japan and Korea. They consist of two species:

1) *S*. *oriens* (Suwa) (= *Lasiomma oriens* Suwa), present in both Japan (Hokkaido island) and Korea (Suwa 1971, 1983a, 1983b; Michelsen, 1988; Kamijo, 1993) (Fig. 1). It is also likely that this species occurs in Far Eastern Russia and Northeastern China (Da Khinggan and Xiao Khinggan Mountains) where typical *Strobilomyia* was observed on firs (Fang *et al*., 1989; Stadnickii *et al*., 1978). In Vladivostok, cone damage was erroneously attributed to *S*. *abietis* Huckett, which is actually endemic to North America (Michelsen, 1988). Hosts include todo-fir, *Abies sacchalinensis* Mast., in Japan and probably Khinggan fir, *A*. *nephrolepis* Maxim., in Siberia and Northeastern China.

2) *S*. *todocola* (Suwa) (= *Lasiomma todocola* Suwa), only recorded from Japan (Hokkaido island) (Suwa, 1971, 1983a; Michelsen, 1988; Kamijo, 1993) (Fig. 6). *Abies sacchalinensis* Mast. is the only known host.

Although not yet observed in a cone, a third *Strobilomyia* species recorded on the island of Hokkaido, *S*. *suwai* Michelsen (Michelsen, 1988), may also be related to firs. Its morphological features closely resemble those of the European fir cone fly, *S*. *carbonaria* (Ringdhal). Other species of fir cone flies probably remain to be discovered, especially in Western and Central China where fir diversity is high. Pan and Roques (2001) noticed that an unidentified species of *Strobilomyia* attacks *Abies georgii*, *A*. *georgii* var. *smithii* and *A*. *delavayi* in the regions of Dali and Lijiang in Yunnan. Damage by *Strobilomyia* sp. was also observed on Siberian fir, *A*. *sibirica*, in the Western Sayan, Central Siberia (Battisti *et al*., 1998).

3.2 Morphology of adults, eggs, larvae and pupae

Adult morphology of *S*. *oriens* and *S*. *todocola* was detailed by Suwa (1971, 1983a). Both species are larger than those attacking larch and spruce cones. Body size ranges from 7 – 7.7 mm in length and wings are 6 – 6.8 mm long, with a proportionally small head and long legs. Ground colour is blackish with thorax and abdomen greyish pruinose. Wings are slightly darkened with a yellowish base. *S*. *suwai* is smaller (wing length 4.4 mm), with a thorax thinly dark greyish brown pruinose (Michelsen, 1988). Wings are brownish black fumose, contrasting with orange-brown calyptrae. Differences in male genitalia allow easy identification of species (Fig. 2) but only the female genitalia of *S*. *oriens* are known (Fig. 3).

Full-grown 3rd-instar larvae of *S*. *oriens* and *S*. *todocola* are 9 – 10 mm long, and thus larger than larch cone maggots. The anterior spiracles also show a larger number of stigmae in fir cone flies (22 – 24 vs. 14 as *S*. *abietis* reported by Stadnitckii *et al*., 1978). The other developmental stages of both species have not been precisely described.

3.3 Biology and phenology

The life cycle of both species appears quite similar. *S*. *oriens* emerge in late May to early June in Primorié and Sakhalin (Stadnitckii *et al*., 1978), but emergence may be delayed at higher latitudes. Adults of *S*. *todocola* also emerge from 20 May to early June in Japan (Kamijo, 1993). Females oviposit at the end of the pollination period of firs. Eggs are usually laid between cone scales, near the cone apex. Soon after hatching, the second-instar larvae enter a cone scale. During June and early July, larvae tunnel into the cone around the axis, feeding on both cones and seeds. In Japan, mature 3rd-instar larvae begin to leave cones to pupate in the ground by early July. In the Xiao Khinggan Mountains of China, all larvae have left by late July cones. A part of the population remains in prolonged diapause the following year (Kamijo, 1993).

Fir cones attacked by cone flies are easily recognized by external examination. As a result of larval

feeding, the upper part of the cone frequently dries out prematurely whereas the mid- and basal part is still green. Moreover, the surface of the damaged parts shows one to several large globular masses consisting of a mixture of cone resin and liquid insect excrement. The mass, of dirty yellow to orange-brown colour, may measure up to 10 cm in diameter.

3.4 Damage importance

Cone flies are major pests of fir seeds in the Far East. Stadnitckii *et al*. (1978) estimated that individual larvae of *S. oriens* (as *S. abietis*) destroy an average of 70 seeds per cone in Primorié. In Sakhalin, *S. oriens* attacked 10% of cones during heavy cone crops but 40% to 95% of the cones were infested, with up to 5 larvae per cone, when the cone crops were light (Stadnickii *et al*., 1978). In Northeastern China, about 45% of the cones were infested in the Xiao Khinggan Moutains (Fang *et al*., 1989). In Japan, *S. todocola* destroys up to 50% of the cones of light to moderate crops (Kamijo, 1993). In Yunnan, 25% to 55% of the cones of *A. georgii* and *A. delavayi* were attacked by *Strobilomyia* sp. (Pan and Roques, 2001).

3.5 Control measures

None yet tested.

4 SPRUCE CONE FLIES

Only 16 papers have dealt with spruce cone flies in the Far East.

4.1 Distribution, hosts and specific identity

Only one species of spruce cone fly, *S. anthracina* (Czerny) (= *Hylemia anthracina* Czerny, *Pegohylemia anthracina* Czerny), is clearly identified in the Far East. It is a Palaearctic species recorded throughout the range of spruce from Western Europe to Japan, including Central Siberia (Evenkiya, Bolshaya Murta), Eastern Siberia, Sakhalin, and Northeastern China (the Da Khinggan and Xiao Khinggan Mountains) cones (Grebenshchikova, 1966; Popova and Elberg, 1970; Suwa, 1971, 1974; Stadnistskii *et al*., 1978; Fan *et al*., 1982, 1990; Nakrokhina, 1983; Fang, 1987; Fang *et al*., 1988, 1989; Michelsen, 1988; Kamijo, 1993; Sun *et al*., 1994; Roques *et al*., 1996a; Belova *et al*., 1998) (Fig. 1). Hosts include Siberian spruce, *Picea obovata* Ledeb., and the Far Eastern spruces, *P. koraiensis* Nakai, *P. ajanensis* Fisch., *P. jezoensis* (Sieb. *et* Zucc.) Carr., and *P. glehnii* (Fr. Schmidt) Mast.

Another species, *S. svenssoni*, is suspected to attack spruce cones (Michelsen, 1988). It has been reared from larch cones in Northeastern China (cf. above) but no conclusive evidence has been yet obtained from spruce. Belova *et al*. (1998) obtained adults from puparia collected under Siberian spruce trees in Central Siberia but noticed that spruce and larch were growing together in the area. However, they found two types of eggs in the spruce cones. One type corresponded to the egg of *S. anthracina* but the other did not resemble that of *S. svenssoni* described from China (Sun *et al*., 1996a). Therefore, another species probably exists in Central Siberia at least. In addition, typical spruce cone fly damage was observed on *Picea likiangensis* in northeastern Yunnan (Pan and Roques, 2001) but adults have not yet been obtained.

4.2 Morphology of adults, eggs, larvae and pupae

Adults are medium-sized flies with a wing length of 4.3 – 5.9 mm. The thorax is finely dark-brownish, grey-pruinose over a shiny black ground colour. Wings are tinged with greyish to brownish black. Calyptrae are light grey to dark brown fumose. Abdomen is shining black. Genitalia easily separate *S. anthracina* from the other *Strobilomyia* species (Figs. 2 – 3).

The egg is whitish, with a smooth chorion. It has an elongate shape, and it measures 1.5 mm on the average. The other type of egg found in spruce cones in Siberia differs in having a chorion marked by a network of hexagonal cells arranged in transverse rows and an average length of 1.7 mm (Belova *et al*., 1998).

Mature 3rd-instar larvae are 7.0 – 9.0 mm long. The anterior spiracles have 16 – 19 stigmae (Skhuravá and Roques, 2000), i.e., a number intermediate between fir cone flies and larch cone flies.

4.3 Biology and phenology

Life cycles in the Far East appears similar to those

observed in Europe (Stadnitckii *et al*., 1978; Kamijo, 1993; Sun *et al*., 1994). Adult flight occurs in spring, immediately following the flushing of female buds and continues until cones turn down. Females lay eggs between the cone scales, close to the cone axis. Only 1 – 3 eggs are usually laid per cone but the number of eggs per cone is higher (6 – 10) when the cone crop is light. The second-instar larva hatches 10 – 12 days following egg-laying and immediately enters a cone scale where it tunnels down toward the base. Once arriving at the scale base, it feeds on the seeds and, then, tunnels around the axis. Sometime the larval gallery cuts the cone axis and thus the cone growth is prematurely stopped. Larval development within the cone lasts about 25 – 30 days. Then, the larva drops to the ground where it builds a puparium to overwinter. Larval exit occurs from late June to late July depending on latitude. A portion of the larval population extends the winter diapause for an additionnal 1 – 3 years, in relation with the fluctuations in the annual cone crop. When the cone crop largely decreases from one year to the next, the major part of the fly population enters prolonged diapause.

Attacked spruce cones are easily recognizable by the presence of large resin masses on the cone surface. The orange-brown resin mass consists of a mixture of cone resin and liquid maggot excrement, and progressively enlarge from 2 – 5 mm in diameter (2nd-instar larva) to 10 – 15 mm (full-grown 3rd-instar larva). However, this typical damage was not observed in Japan (Kamijo, 1993). As a result of larval feeding, the cone is usually curved and its damaged part (usually the apex) dries out prematurely, turning a brown or black colour whereas the undamaged parts remain green.

4.4 Damage importance

This species is a major seed pest of spruce. In Siberia, a larva destroys 40% – 45% of the seeds in a cone of *P. obovata*. When 2 – 3 larvae are present, damage reaches 60% – 73% but this actually results in a total loss of seed content because undamaged seeds will not disperse (Stadnickii *et al*., 1978). In Northeastern China (Da Khinggan Mountains), the percent of damaged cones of *P. koraiensis* varied between 2.5 and 31.2 according to stand (Sun *et al*., 1994). In Japan, damage to cones of *P. jezoensis* and *P. ghlenii* ranged 21% – 55% in years of light cone crops but decreased to 10% when the cone crop was heavy (Kamijo, 1993). In Yunnan, 15% to 40% of the cones of *P. likiangensis* were attacked by *Strobilomyia* sp. (Pan and Roques, 2001).

4.5 Control measures

No control measures have yet been applied in the Far East. However, the effect of both larval parasitism and fungal disease on *Strobilomyia* survival has been noticed in Central Siberia where these factors account for the death of 28.1% and 24.8% of pupae respectively (Belova *et al*., 1998). Recorded parasites consist of *Phaenocarpa* sp. (Braconidae) in Central Siberia and in the Irkustk region, and *Seitneria* sp. (Cynipidae) in Central Siberia (Golutvina, 1973; Belova *et al*., 1998).

5 CONCLUSION

The specific biological features of most cone fly species are quite clearly established. However, confusion remains about the identification of larval stages and the estimation of subsequent damage caused by larch cone flies. Most data generally still rely on the posteriori measure of the relative emergence of adult flies which can be easily identified by their genitalia. Because of the prolonged diapause phenomenon and possible differential mortality during this phase, the specific percentage of emerged adults may not accurately reflect specific damage in previous years. The development of easy-to-use tools for accurate identification of larvae within the cone would thus represent real progress. The current development of genetic studies is also likely to result in some changes to *Strobilomyia* taxonomy, and to give interesting information about the evolutionary relationships between conifer hosts and cone fly species, e. g., why are there so many species related to *Larix* but not *Picea* and *Abies*? Finally, it is quite certain that several other cone flies are yet to be described, especially in the Hymalayan range.

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远东地区影响针叶树天然更新的球果种实害虫
——球果花蝇（双翅目：花蝇科）

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摘要：球果花蝇是远东地区的重要球果种实害虫。尤其是在我国东北地区，由于球果花蝇的危害已严重影响了落叶松种子产量，进而影响到落叶松的造林与更新。本文系统地总结了近些年危害落叶松、云杉、冷杉种实的球果花蝇的研究进展及存在的问题。文中还涵括了作者的一些原始研究数据和尚未发表的新结果。

关键词：针叶树；球果；种实；球果花蝇；球果花蝇属

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